

molli wrote, "The last word will however only be said after a complete revision of all the genera of Cheilantheae, which, as usually construed, are certainly neither naturally nor conveniently classified." And now we have lost the man best qualified for such a revision.

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## The Habitat of *Diellia*

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The Hawaiian fern genus *Diellia* has been beset with problems for the taxonomist and morphologist for many years. Doubts have been expressed repeatedly by various authorities as to whether its "species," eight in all, have any real validity. Its generic relationships have been interpreted as being with the pteroid ferns (especially *Lindsaea*), the davallioid ferns (*Davallia*, *Humata*, and *Nephrolepis*), and more recently with the asplenioid ferns, *Asplenium* and *Loxoscaphe*. These wide discrepancies in interpretation have been based on the sorus structure, the frond habit, and scales.

Underlying these problems has been the excessive scarcity of materials of this genus in herbaria, and in nature. It is generally believed to be on the verge of extinction. Modern, complete collections are few, and most of our ideas of the diversity within the genus are based on isolated fragments collected in the period 1850-1880. The most recent attempt to study *Diellia* was made by the late Dr. Frances G. Smith whose report was briefly reviewed by Mr. Weatherby.<sup>1</sup> Dr. Smith concluded from her lack of success in finding materials in the field and in aligning what specimens did exist in herbaria that the problems of this genus might never be

<sup>1</sup> This JOURNAL 25: 103, 104. 1935.

settled and that *Diellia* was dying out.<sup>2</sup> Therefore, in 1947 and again in 1949, investigations of this genus were made under auspices of the University of California Department of Botany with the cooperation of Dr. H. St. John of the University of Hawaii and Miss Marie C. Neal of the B. P. Bishop Museum. Dr. H. L. Lyon has kindly contributed considerable information. In view of the rarity of the genus, it is believed that this summary of results in getting information on its occurrence in nature will be a contribution to our knowledge of these peculiar Hawaiian ferns.

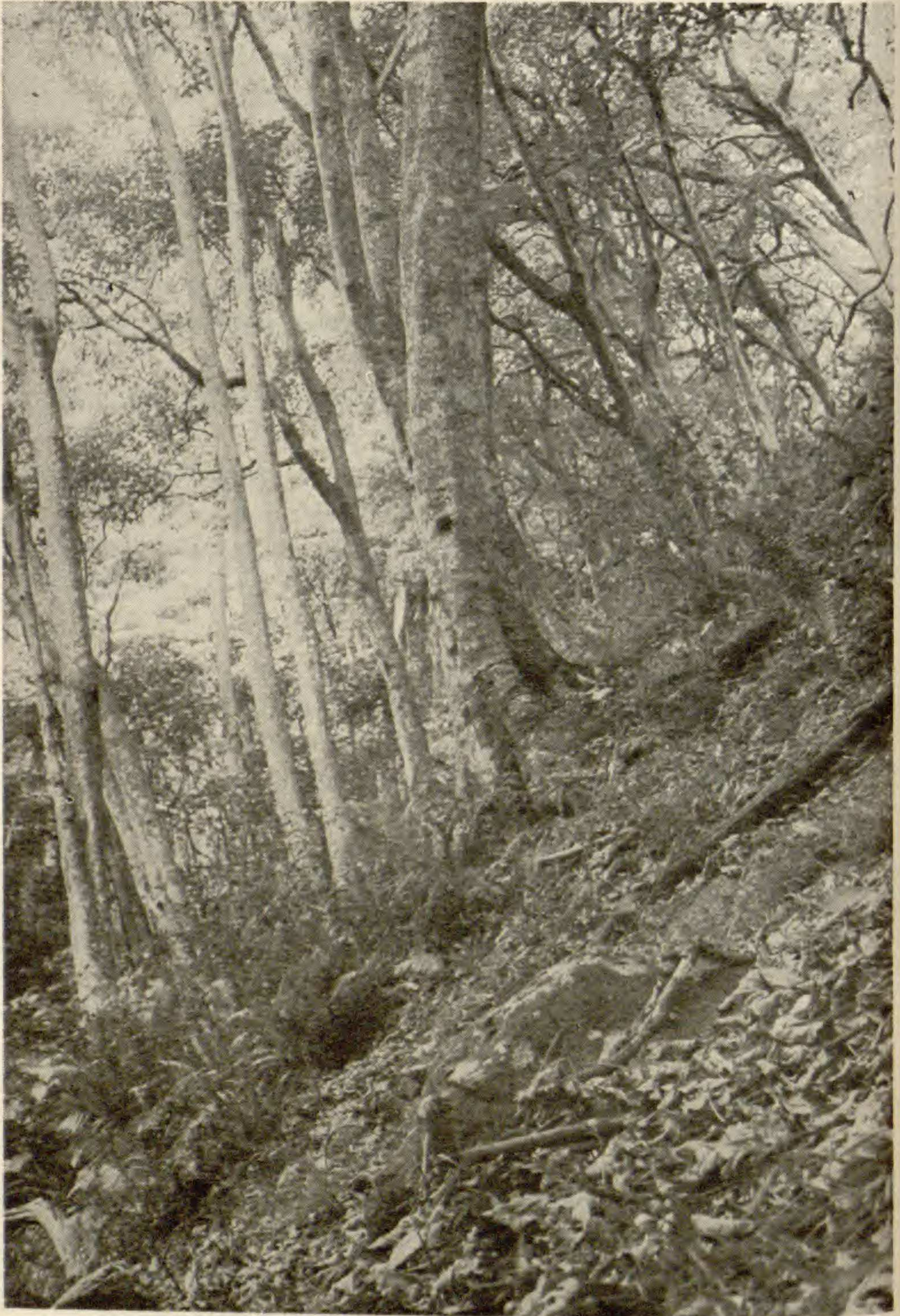
Few herbarium sheets made before 1900 give localities; of modern ones only few include data complete enough to guide the collector to appropriate habitats. The literature is usually vague or misleading regarding habitats. Brackenridge, who described the genus in 1854, gave for *Diellia erecta* the habitat "in mountain forests of the western division of Maui"; for *D. falcata*, "Kaala Mountains, Oahu . . ., on open and dry rocky ridges; rare"; and *D. pumila*, "Oahu . . ., in the crevices of rocks; rare." In 1867, Mann gave the habitat of *D. Mannii* (as a *Microlepia*) as "Waimea, Kauai, 2000-3000 ft." This species has not been found since 1900, but the altitudes given suggest it was a fern of the arid western "plateau" region of Kauai, well below the rain-forest. Support is given this belief by Hillebrand's addition in 1888 of Halemanu, Kauai, as a locality. That this spectacular fern with fronds 4-5 times pinnate and stipes of shiny dark-purple was uncommon even then is suggested by Diel's reference to it only 14 years later as a "Seltenheit Kauais."

For *Diellia Alexandri* (as *Davallia*) Lidgate in 1873 gave "Haleakala, 3,000 to 4,000 ft," and Hillebrand

<sup>2</sup> *Diellia* and its variations. B. P. Bishop Museum Occ. Papers 10, No. 16: 1-22. 1934.

(calling it *Lindsaea*) later added "northern slope." But to the investigator seeking the exact spot, it would have been necessary to refer to a popular book, "Aló-ha!", published in 1879 by A. L. Chaney. Here, in discussing the prevalent sport of the day—fern-hunting—the writer revealed the exact gulch (p. 253). Further habitat notes on *D. pumila* are confusing: Bailey said it grew on the "damp side of gulches" in 1883, and Hillebrand in 1888 called its habitat "exposed cliffs." Rock in 1913 said that "*Diellia* has several species peculiar to Kauai, as *D. centifolia*, *D. laciniata*, and *D. Knudsenii*, which belong to the swampy region." MacCaughey in 1918 included *Diellia* in his third class, "species which are characteristic of the middle forest zone—the rain-forests on the mountain slopes which lie between 1800 and 3000–5000 ft." *D. erecta* was in his fourth class, "a region of torrential rain," but *D. pumila* and *D. falcata* were "distinctly xerophytic." These conflicting reports actually give no real picture of the habitat of *Diellia*. For some of them there is no evidence at all. It is my belief that all of the "species" of this genus occur or occurred in the same basic type of habitat. This is concluded from a study of ten localities on four islands, and a compilation of what accurate data are on labels. Only one description of a habitat known to me gives a clear picture, that of C. G. Munro on the island of Lanai, quoted by Smith. A general description of the occurrence of *Diellia* follows.

*Diellia* is endemic to the larger Hawaiian islands. A fern named in this genus, *D. Brownii* E. Brown from the Marquesas has since proved to be a *Nephrolepis*. Using a broad species interpretation and construing *D. erecta* to include such forms as *D. Alexandri*, *D. pumila*, *D. centifolia*, and *D. laciniata*, then it is a polymorphic species known from the islands of Kauai, Oahu, Molokai,



TYPICAL *DIELLIA* HABITAT, MAHANALOA VALLEY, KAUAI

Lanai, Maui, and Hawaii. On Kauai *D. Mannii* (including *D. Knudsenii* as the juvenile form) and an apparently undescribed species found in 1947-49 are both endemics. Oahu has the one remaining species, *D. falcata*, as an endemic. Localities known today range in altitude from 1250 to 3700 ft. All of the stations are in more or less arid regions. Comparison with maps of isohyet lines of the islands shows that annual rainfall at *Diellia* localities ranges from about 35 to 80 inches. Temperature estimates based on Weather Bureau records from stations at different altitudes would range from 70° to 62° F. with increasing elevation. Many of the localities lie in Ripperton and Hosaka's "Zone C," an area running to a maximum of 4000 ft., with a natural cover of "Mixed open forests and shrubs." Two stations on Molokai and two on Maui are in their "Zone D," an area of shrub and closed forest with 60 or more inches of rain. Most localities are on lee sides of mountains, and those facing northeast toward the trades are protected by other mountains lying windward which cut down rainfall.

Within these relatively arid regions, this genus is confined usually to steep gulch sides (*Pl. 2*). In numbers of plants, a given locality may have from one or several to thousands, but the populations are always local or "spotty" and usually small. The plants are inconspicuous and resemble casually such ferns as *Nephrolepis*, *Asplenium*, and *Doodia*. A typical gulch or canyon where *Diellia* occurs is one with sides more or less wooded or shrub-covered and sloping from nearly vertically to about 30° or 40°. The stream bed at the bottom is usually dry or at least without flowing water most of the year. In all cases the soil is somewhat rocky, the particles of rock ranging in size from less than a centimeter to three or four feet in diameter.



ABOVE: *DIELLIA ALEXANDRI*, GROWING ON SHADED ROCK SHELF,  
E. MAUI (PHOTOGRAPH BY JOHN B. BONSEY)  
BELOW: *DIELLIA FALCATA*, GROWING ON OPEN SOIL, OAHU  
(PHOTOGRAPH BY CHARLES E. ST. JOHN)

Plants are commonly found growing directly on rock surfaces (*Pl. 3*) in crevices or ledges, or on open soil (*Pl. 3*). The rock is mostly of a soft *aa* type. The soil reaction in all such places tested (with a LaMotte Soil "Teskit") was of pH 7.0–8.0. When the plants grow directly on soil, this is always loose, dry, and granular, i.e. tends to hold together in small lumps. It appears to be well aërated, with quick drainage.

The plants grow in the shadow of overhead trees or smaller plants. *Aleurites moluccana*, the *kukui*; *Metrosideros polymorpha*, the *lehua*; *Psidium Guayava*, *guava*; and *Acacia Koa*, the *koa*, are commonly associated trees. Others reported are *Pisonia* (Munro) and *Bobea* (Degener). Of smaller plants, *Eupatorium adenophorum*, the *pamakane*, is an especially common provider of shade for *Diellia erecta* and its forms on Molokai and in east Maui. On Oahu a coarse grass, *Eragrostis* sp. (Wagner 5801) provides shade on open hillsides of the western side of the Waianae Range for a tiny form of *Diellia*. In no case were plants found exposed to full sunlight.

Where *Diellia* occurs a variety of other ferns, to be discussed, as well as flowering plants make up the understory. Toward the bottoms of the gulches the understory becomes increasingly dense as the amount of soil water increases and shade becomes deeper. In the gulch bottoms themselves such ferns as *Athyrium* spp. and *Pteris excelsa*, not found on the slopes, form dense ground covers. At the tops of the slopes, on the contrary, the situation is usually so dry and exposed that few ferns other than bracken are found. *Diellia* usually exists between these extremes, and the level on the sides of gulches at which its species attain their best development is usually in a broad horizontal band with its center line halfway up the slope. Juvenile plants are often seen, and occasionally adults, on rocks or soil banks

(*Pl. 4*) at the bottoms of gulches where these are rather open, but it was discovered that if one climbed the slopes (mostly north-facing ones) from 20 to 150 feet above these plants that more numerous and older individuals would be revealed.

All of the habitats showed disturbance, and this appears to be very important. Although plants were frequently seen on bare or slightly mossy rock surfaces of relatively permanent boulders or rock outcrops (*Pl. 3*), all plants on soil surfaces were found in disturbed places and were apparently temporarily free from competition of the other understory plants. Presumably in most of these places the common understory plants will ultimately return and crowd out *Diellia*. One of the largest colonies of this genus found at Puu Kolekole, Molokai, grew on a steep rock-slide which probably originated in the last decade. *Eupatorium adenophorum* has since established itself on the "slide" and provided shade for plants of *Diellia*. A similar but much more recent "slide" or avalanche, of about 15 by 30 feet, was nearby, but no plants had yet made a start here. Situations at Paaiki and Mahanaloa Valleys, Kauai, and Haleanu Gulch (*Pl. 4*), and Pohakea Pass, Oahu, similarly showed a greater or lesser movement of rocks and soil down the steep slopes—a movement which is constantly going on sporadically and which exposes small areas of soil and rock surface. The unsettled nature of these places is such that the collector must often hold on to branches and roots of trees so as not to slide down the slope along with the readily dislodged rocks and soil. Situations like this in the primeval Hawaiian canyons very likely provided the new soil surfaces, small areas temporarily free of other understory vegetation, which these plants seem to require. Likewise, old and crumbling *aa* lava flows such as those at Manuka, Kau Dis-



tract, Hawaii, where G. W. Russ found this plant, offered natural habitats for *Diellia*.

In modern times, however, new surfaces may be cleared off locally by activities of cattle or goats, or by maintenance of foot- or horse-trails in wooded gulches. A number of collections illustrate this: Dr. H. L. Lyon kindly informed me that cattle paths traversed the area where he found *Diellia falcata* at Makaleha, Oahu. A specimen of C. G. Munro from Lanai of *D. erecta* (B. P. Bishop Museum) is labeled "near waterhole," and a collection of Degener and Topping from near Kawaihapai, Oahu, is labeled as coming from "moist rocks in arid woods near watering trough." In the period when most of the collections of this genus (*D. Mannii*, *D. laciniata*, *D. Alexandri*, *D. centifolia*, *D. Knudsenii*) were made around Halemanu, Kauai, by Knudsen about 1875, cattle were numerous there, and travel was made along horse-trails. It seems very probable that this enabled *Diellia* to grow at that time in the ravines there, in places now once again grown over since the cattle were removed years ago. More permanent native vegetation as well as various exotics have now crowded out *Diellia* at Halemanu and Kokee. At Piiholo, Maui, and Puu Kolekole, Molokai, cattle and goat trails criss-cross along the slopes and the majority of the plants found at these places occurred under these disturbed conditions. At two spots near Puu Kolekole where fences cross the wooded or shrubby gulches obliquely, trails of cattle and goats following the fences toward water-holes at the gulch bottoms increased to a large number and here plants were very numerous, especially immature ones (*Pl. 4*). Maintaining foot-trails through wooded gulches has the same effect. At Kahuaawi Gulch, Molokai, the only large plants seen were on low boulders just beside a foot-trail which had been kept up for nine years; a



SPORELINGS OF *DIELLIA ERECTA* ON DRY DIRT BANK, MOLOKAI

careful search in the understory nearby revealed no *Diellia*, apparently because the ground cover of *Nephrolepis* (particularly) and other ferns and flowering plants was too dense.

Thus, temporarily disturbed areas have proved to be the usual habitat, and the sources of this disturbance are in the following categories: (1) by natural rock slides or avalanches, and decaying *aa* flows, (2) by destruction of understory cover and induced rock slides (a) from domestic or feral animals, and (b) by man-made trails.

Usually other fern genera are not growing immediately with *Diellia*, but a number of ferns regularly occur near it. I found it convenient to use these associated ferns as "indicators" in seeking localities for *Diellia*, with recognition of possible fallacies in such a procedure. These ferns were *Nephrolepis exaltata*, *Doodia Kunthiana*, *Doryopteris* spp., *Asplenium Macraei*, *A. Adiantum-nigrum*, *Phanerophlebia caryotideia*, *Microlepia strigosa*, and the *Pteris cretica* complex. The ubiquitous *Psilotum nudum* is almost always near by, and such spleenworts as *Asplenium unilaterale*, *A. horridum*, *A. enatum*, *A. contiguum*, and *A. acuminatum* are occasionally on the same slopes. Each of these ferns, to be sure, has its own specific tolerance ranges for factors of the Hawaiian environment: for instance, while *Nephrolepis exaltata* and *Asplenium unilaterale* extend into the wet forest, *A. Adiantum-nigrum* and the species and forms of *Doryopteris* are confined strictly to the arid regions. *Asplenium Macraei*, *Phanerophlebia caryotideia*, and the group of *Pteris cretica* seem to approach *Diellia* the most closely. Somewhere in the complex overlap of the various environmental requirements of all these ferns listed is the typical physiological situation for *Diellia*, and I believe that any situation possessing the physical features de-

scribed earlier, and supporting most of the ferns listed above, should be investigated as a likely habitat for this genus anywhere in the Hawaiian Islands.

From this summary it may be concluded that the habitat of *Diellia* is a transient one, both edaphically and biotically, which occurs constantly but sporadically, both in time and area, through the steep and dryer wooded gulches of the Hawaiian Islands. It may be surmised that the apparent rarity of the genus is due to the relatively small areas that such suitable environments occupy at any one time. The "disappearance" of the genus from some of its former localities may be due to the removal of disturbing influences which provided appropriate edaphic and biotic conditions. On the face of present evidence it does not follow that the genus is "on the verge of extinction." Because its habitat is transitory, it has probably always been rare and local! Further field research may even reveal that *Diellia Mannii* still exists somewhere in western Kauai.

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## The Problem of Generic Segregates in the Form-Genus *Lycopodium*<sup>1</sup>

BERNARD BOIVIN

During the academic year of 1947-8, it was my privilege to work under the guidance of the late Mr. C. A. Weatherby as Harvard Research Associate and as a scholar of the John Simon Guggenheim Memorial Foundation. Those of us (nearly every North American Botanist) who have worked with or under Weatherby or who have at one time or another asked him for help or

<sup>1</sup> Contribution No. 1002 Division of Botany and Plant Pathology, Science Service, Dominion Department of Agriculture, Ottawa, Canada.